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Sweet connections: the role of honeydew in supporting wild *Bombus terrestris* populations (Hymenoptera, Apidae) – a case study from Türkiye

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Abstract

Honeydew is a sugary excretion produced by sap-feeding hemipterans, such as scale insects and aphids. It has been regarded predominantly as a food resource for predators and omnivores insects. Its potential role as a food source for pollinators, particularly bumble bees, remains underexplored. This study investigates the foraging of *Bombus terrestris* (L.) on honeydew secreted by *Sphaerolecanium prunastri* on *Prunus cerasifera* in a semi-natural environment. Field observations revealed that *B. terrestris* workers actively forage on honeydew. These findings indicate that *B. terrestris* is capable of utilizing honeydew as an alternative foraging resource. Additionally, our results suggest species-specific preferences for honeydew among bumble bee species, underscoring the complexity of plant-insect interactions. This is the first report of interaction between *B. terrestris* and *S. prunastri*, including the sugar composition of the honeydew and the associated foraging behavior. Understanding how pollinators adapt to alternative food sources like honeydew is essential for predicting their ecological resilience and guiding effective conservation strategies.

Keywords

Coccidae, mutualism, *Prunus cerasifera*, *Sphaerolecanium prunastri*, sugar content

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Plant-insect interactions play a pivotal role in shaping ecosystem structure and function (Dofuor et al. 2024). The categorization of insects as beneficial or harmful is shaped by human-centric perspectives. This is especially the case in agricultural contexts, where their roles are primarily defined based on contributions to crop production and pest control.

Bumble bees (Apidae: *Bombus*), for instance, are important pollinators for both wild and cultivated crops. Traits such as buzz pollination and foraging at lower temperatures distinguish them from other pollinators (Goulson 2010). *Bombus terrestris* (L. 1758) (Hymenoptera: Apidae), the buff-tailed bumble bee, is one of the most widespread species in the Western Palaearctic and a crucial pollinator. It is native to temperate Eurasia and widely introduced elsewhere for crop pollination (Rasmont et al. 2008; Herbertsson et al. 2021).

In contrast to pollinators, scale insects such as the Globose Scale *Sphaerolecanium prunastri* (Boyer de Fonscolombe, 1834) (Hemiptera: Coccidae), are considered harmful as they use their mouthparts to pierce the plant tissue to reach the phloem sap of the host plant, causing tissue damage. The excretion of honeydew can coat the branches and leaves of the plant and facilitate the growth of sooty mold, which further reduces the plant's photosynthetic capacity (Durovic and Ülgentürk 2014, 2021; Álvarez-Pérez et al. 2024).

Although honeydew production can have detrimental ecological consequences, this carbohydrate- and amino acid–rich substance can be an important alternative food source for some pollinators in a complex ecological association between honeydew-producing insects and their consumers (Dhami et al. 2011; Meiners et al. 2017). Many animals exploit honeydew as a nutritional resource. A well-known example is the mutualistic interaction between aphids (Hemiptera: Aphididae) and ants (Hymenoptera: Formicidae), in which ants protect aphid colonies in exchange for honeydew (Mouratidis et al. 2021; Nelson and Mooney 2022). Additionally, lepidopterans, spiders, neuropterans, and various hymenopterans consume honeydew, though often indirectly (Hogervorst et al. 2008; Pfannenstiel 2015; Sakagami and Sugiura 2018). The relationship between the pine scale *Marchalina hellenica* (Hemiptera: Marchalinae) and the honey bee *Apis mellifera* L. (Hymenoptera: Apidae), which produces pine honey from collected honeydew, is well documented in Greece and Türkiye (Gounari 2006; Ülgentürk et al. 2021). However, observations of bumble bees utilizing scale honeydew remain scarce. Evidence suggests that aphid honeydew may act as a substitute resource when floral nectar is limited. For example, Cameron et al. (2019) proposed that climate-induced stressors, including heat and drought, can shift *Bombus terrestris* foraging toward non-floral, sugar-enriched evaporated aphid honeydew. Batra (1993) reported that *B. terricola* workers in alpine tundra regions consumed honeydew produced by *Mindarus abietinus* aphids. Similarly, Percy and Cronk (2022) reported bumble bees feeding on honeydew produced by aphids in proximity to *Melilotus albus* Medik. (Fabaceae).By utilizing honeydew as an alternative energy source, bumble bees may mitigate the effects of resource shortages, while providing a cleaning service to the plant by consuming honeydew that might otherwise foster the growth of harmful

molds (Banerjee et al. 2024). If so, this poses a mutualistic dynamic similar to the well-known ant-aphid interaction (Rice and Eubanks 2013).

A deeper understanding of the interactions between pollinators and honeydew-producing insects calls for exploration of ecological implications, particularly ecosystem resilience and adaptation of pollinators in response to environmental changes.

Toward this end, we present observations on the foraging of *B. terrestris* on honeydew produced by *S. prunastri*, including an analysis of the honeydew's sugar composition.

Our study site was the campus of Hacettepe University, Ankara, Türkiye, which spans approximately 10 km^2 and is bordered by pine plantations interspersed with open areas characterized by steppe vegetation. The campus flora comprises 510 taxa belonging to 57 families, including 65 native and endemic to Türkiye and 145 cultivated species (Mutlu et al. 2008). *B. terrestris*, *B. niveatus*, *B. argillaceus*, and *B. zonatus* are distributed throughout the area (Özenirler 2025).

In June 2024, approximately 20 workers of *B. terrestris* were observed feeding on honeydew produced by *S. prunastri* on *Prunus cerasifera* Ehrh. (Fig. 1a, b). Female scales were collected in 75% ethanol and identified to species following Kozar and Kosztarab (1988). The bumble bees were identified according to Rasmont et al. (2021). Flowering plants in the study area were determined using the "Flora of Turkey" (Davis 1965–1988; Güner et al. 2000) and "Beytepe Bitkileri" (Akaydın 2011). To analyze honeydew composition, exudates were collected using a 30 × 50 cm glass sheet placed beneath the tree in the observation area between 11:00 and 14:00. Honeydew deposited on the glass surface was retrieved by gently scraping it with a razor blade. The samples were stored at –20 °C and subsequently analyzed for sugar content using high-performance liquid chromatography (HPLC). Glucose, fructose, sucrose, and galactose were quantified in triplicate.

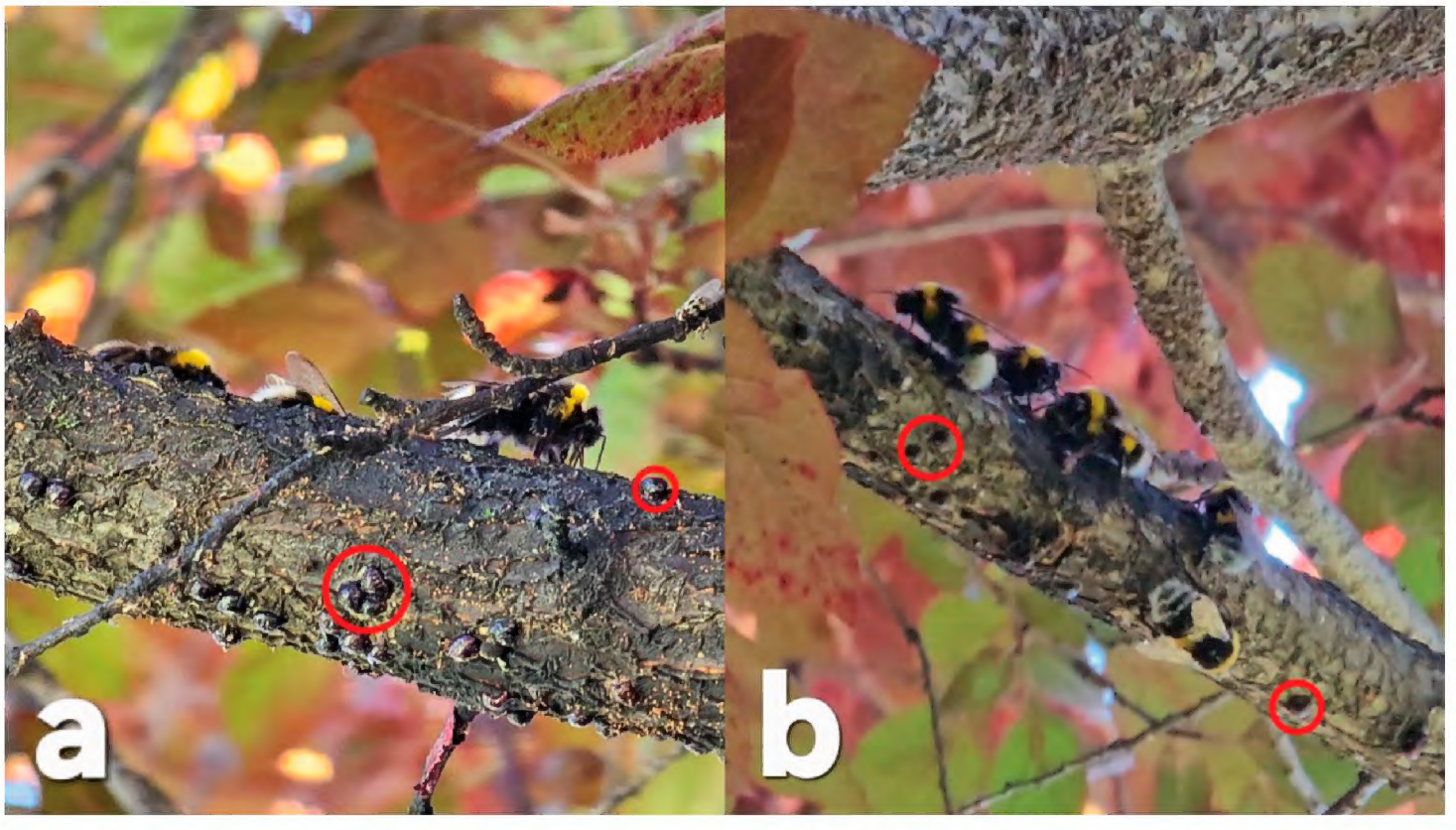

Figure 1. a, b young females of *Sphaerolecanium prunastri* (Coccidae, indicated with red circles) on *Prunus cerasifera* branches and *Bombus terrestris* workers foraging on honeydew.

The host tree was confirmed as *P. cerasifera*. *S. prunastri* colonies consisted mainly of young females located on the undersides of branches. The 20 *B. terrestris* workers were actively collecting honeydew exclusively from branches, even though droplets were also present on leaves. The honeydew contained glucose (13.3 ± 0.1 mg/mL), fructose (4.7 ± 0.0 mg/mL), and sucrose (3.3 ± 0.0 mg/mL), while galactose was undetected. The surrounding semi-natural landscape, enhanced by irrigation and landscaping, supported a rich floral assemblage including *Daucus carota*, *Carduus nutans* var. *nutans*, *Hypericum perforatum*, *Stachys annua* subsp. *annua*, *Convolvulus lineatus*, *Centaurea triumfettii*, *Anchusa azurea* var. *azurea*, *Sideritis montana*, *Salvia absconditiflora*, *Lamium amplexicaule*, *Trifolium* spp., and *Astragalus* spp.

The sugar concentrations detected in *S. prunastri* honeydew were low, with glucose as the dominant sugar. This profile reflects the highly variable and often dilute composition characteristic of scale insect honeydew, shaped by host plant chemistry and insect-specific metabolic processes, rather than indicating strong nutritional value (Beggs et al. 2005; Tena et al. 2013; Pringle et al. 2014; Blanchard et al. 2022). Previous studies on *Coccus* species and other sap-feeding insects have shown that the total sugar content as well as the relative proportions of glucose, fructose, and sucrose can vary substantially among species and host plants, with many scale insects producing honeydew that is more dilute than that of aphids or most floral nectars (Fischer et al. 2005; Wool et al. 2006; Tena et al. 2013). Taken together, these findings suggest that *S. prunastri* honeydew offers *B. terrestris* an extremely modest carbohydrate source with a specific composition. Glucose-rich honeydew provides readily accessible energy, but the relatively low overall sugar concentrations limit its reward value.

The glucose-dominant profile of *S. prunastri* honeydew likely provides bumble bees with a rapid, albeit exceptionally low, energy source during periods of intense activity or reduced floral nectar availability. Although the sucrose concentration is far below that which is optimal for bumble bee foraging (Pattrick et al. 2020), workers were observed collecting honeydew directly from branches.

While it is possible that bees could exploit such dilute honeydew as a water source, we consider this explanation unlikely in the area where we conducted our observations. The research took place in a semi-artificial university campus landscape with regular irrigation and multiple readily available water sources (e.g., ornamental ponds, wet soil, and irrigation runoff), which are commonly used by foraging insects. Therefore, it is more plausible that *B. terrestris* workers were targeting the carbohydrate fraction of honeydew as a supplemental energy source rather than using it primarily for hydration.

This indicates that they are opportunistically foraging for carbohydrate resources. The absence of galactose may reflect taxon-specific metabolic differences in honeydew production. Previous work has shown that *B. terrestris* workers can shift their sugar preference toward fructose after exposure to fructose-rich resources (Meeus et al. 2013), and their dense antennal taste receptors allow detection of even dilute sugar sources (Mommaerts et al. 2013). These traits together indicate that, despite its low sugar content, honeydew can be utilized as an alternative and supplemental resource.

B. terrestris is a polylectic species that exploits a wide range of plant taxa across multiple families in Türkiye (Gürel et al. 2008), as evidenced by the analysis of nest materials at the end of the season, which revealed diverse dietary preferences within the study area (Özenirler 2021). This diversity of pollen sources underscores the ecological plasticity of *B. terrestris*, enabling it to persist under fluctuating environmental conditions and variable floral resource availability.

This dietary breadth reflects the species' ecological plasticity and ability to persist under fluctuating environmental conditions. Interestingly, in this study, honeydew foraging occurred despite abundant floral resources, differing from previous reports that link such behavior to nectar scarcity. This finding suggests that *B. terrestris* may opportunistically exploit honeydew not only as a fallback resource but as part of a broader adaptive foraging strategy in heterogeneous landscapes.

Conclusion

This study demonstrates the foraging plasticity of *B. terrestris*, particularly its ability to exploit *S. prunastri* honeydew as an opportunistic alternative foraging source. Future research should incorporate detailed chemical analyses of honeydew and investigate its ecological role and potential interactions with other wild bee species, thereby providing stronger insights to support pollinator conservation strategies. In addition, evaluating abiotic factors such as temperature and relative humidity will be essential for understanding how environmental conditions influence honeydew availability and bee foraging behavior.

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References

Akaydın G (2011) Beytepe bitkileri [Plants of Beytepe]. Hacettepe University Press.

Álvarez-Pérez S, Lievens B, de Vega C (2024) Floral nectar and honeydew microbial diversity and their role in biocontrol of insect pests and pollination. Current Opinion in Insect Science 61: 101138. https://doi.org/10.1016/j.cois.2023.101138

Banerjee RP, Barik SK, Borges RM, Agrawal M (2024) Plant defence mechanism in honeydew-mediated plant-Hemiptera-ant interactions and ecosystem sustainability: A review. Environmental Sustainability 7: 427–437. https://doi.org/10.1007/s42398-024-00326-8

Batra SWT (1993) Opportunistic bumble bees congregate to feed at rare, distant alpine honeydew bonanzas. Journal of the Kansas Entomological Society 66: 125–127. https://www.jstor.org/stable/25085419

Beggs JR, Karl BJ, Wardle DA, Bonner KI (2005) Soluble carbon production by honeydew scale insects in a New Zealand beech forest. New Zealand Journal of Ecology 29: 105–115. https://www.jstor.org/stable/24056198

Blanchard S, Verheggen F, Van De Vreken I, Richel A, Detrain C (2022) Combined elevation of temperature and CO_2 impacts the production and sugar composition of aphid honeydew. Journal of Chemical Ecology 48: 772–781. https://doi.org/10.1007/s10886-022-01385-z

Cameron SA, Corbet SA, Whitfield JB (2019) Bumble bees (Hymenoptera: Apidae: *Bombus terrestris*) collecting honeydew from the giant willow aphid (Hemiptera: Aphididae). Journal of Hymenoptera Research 68: 75–83. https://doi.org/10.3897/jhr.68.30495

Davis PH [Ed.] (1965–1988) Flora of Turkey and the East Aegean Islands (Vols 1–10). Edinburgh University Press.

Dhami MK, Gardner-Gee R, Van Houtte J, Villas-Bôas SG, Beggs JR (2011) Species-specific chemical signatures in scale insect honeydew. Journal of Chemical Ecology 37: 1231–1241. https://doi.org/10.1007/s10886-011-0030-5

Dofuor AK, Osei-Owusu J, Osabutey AF, Lutuf H, Antwi-Agyakwa AK, Andoh-Mensah S, Asante K, Aidoo OF (2024) Plant-insect interactions under agroecosystems: an overview of ecological implications for future research. Cogent Food & Agriculture 10: 2379606. https://doi.org/10.1080/23311932.2024.2379606

Durovic G, Ülgentürk S (2014) Ballı madde salgısı. Türkiye Entomoloji Bülteni 4(2): 121–137. https://doi.org/10.16969/teb.67717

Durovic G, Ülgentürk S (2021) Description of globose scale immatures stages (*Sphaerolecanium prunastri* (Boyer de Fonscolombe) (Hemiptera: Coccidae). Yuzuncu Yıl University Journal of Agricultural Sciences 31: 982–994. https://doi.org/10.29133/yyutbd.989768

Fischer MK, Völkl W, Hoffmann KH (2005) Honeydew production and honeydew sugar composition of polyphagous black bean aphid, *Aphis fabae* (Hemiptera: Aphididae) on various host plants and implications for ant-attendance. European Journal of Entomology 102: 155–160. https://doi.org/10.14411/eje.2005.025

Goulson D (2010) Bumblebees: Behaviour, Ecology, and Conservation (2nd edn.). Oxford University Press. https://doi.org/10.1093/oso/9780199553068.001.0001

Gounari S (2006) Studies on the phenology of *Marchalina hellenica* (Hemiptera: Coccoidea, Margarodidae) in relation to honeydew flow. Journal of Apicultural Research 45: 8–12. https://doi.org/10.1080/00218839.2006.11101305

Gürel F, Gosterit A, Eren Ö (2008) Life-cycle and foraging patterns of native *Bombus terrestris* (L.) (Hymenoptera, Apidae) in the Mediterranean region. Insectes Sociaux 55: 123–128. https://doi.org/10.1007/s00040-008-0984-7

Güner A, Özhatay N, Ekim T, Başer KHC, Hedge IC [Eds] (2000) Flora of Turkey and the East Aegean Islands (Vol. 11, Suppl. 2). Edinburgh University Press.

Herbertsson L, Khalaf R, Johnson K, Bygebjerg R, Blomqvist S, Persson AS (2021) Long-term data shows increasing dominance of *Bombus terrestris* with climate warming. Basic and Applied Ecology 53: 116–123. https://doi.org/10.1016/j.baae.2021.03.008

Hogervorst PAM, Wäckers FL, Carette AC, Romeis J (2008) The importance of honeydew as food for larvae of *Chrysoperla carnea* in the presence of aphids. Journal of Applied Entomology 132: 18–25. https://doi.org/10.1111/j.1439-0418.2007.01247.x

Kozar F, Kosztarab M (1988) Scale Insects of Central Europe. Akademia Kiado (Budapest), 1–456. https://doi.org/10.1007/978-94-009-4045-1

Meiners JM, Griswold TL, Harris DJ, Ernest SM (2017) Bees without flowers: before peak bloom, diverse native bees find insect-produced honeydew sugars. American Naturalist 190: 281–291. https://doi.org/10.1086/692437

Meeus I, Mommaerts V, Billiet A, Mosallanejad H, Van de Wiele T, Wäckers F, Smagghe G (2013) Assessment of mutualism between *Bombus terrestris* and its microbiota by use of microcolonies. Apidologie 44: 708–719. https://doi.org/10.1007/s13592-013-0222-9

Mouratidis A, Vacas S, Herrero J, Navarro-Llopis V, Dicke M, Tena A (2021) Parasitic wasps avoid ant-protected hemipteran hosts via the detection of ant cuticular hydrocarbons. Proceedings of the Royal Society B 288(1942): 20201684. https://doi.org/10.1098/rspb.2020.1684

Mommaerts V, Wäckers F, Smagghe G (2013) Assessment of gustatory responses to different sugars in harnessed and free-moving bumble bee workers (*Bombus terrestris*). Chemical Senses 38: 399–407. https://doi.org/10.1093/chemse/bjt014

Mutlu B, Erik S, Tarıkahya B (2008) New contributions to the flora of Beytepe Campus Ankara and floristic comparison with neighboring floras and other campus floras. Hacettepe Journal of Biology and Chemistry 36.3: 181–195.

Nelson AS, Mooney KA (2022) The evolution and ecology of interactions between ants and honeydew-producing hemipteran insects. Annual Review of Ecology, Evolution, and Systematics 53: 379–402. https://doi.org/10.1146/annurev-ecolsys-102220-014840

Özenirler Ç (2021) Detection of plant species visited by *Bombus terrestris* (L. 1758) (Hymenoptera: Apidae) via pollen analysis from nest materials. Biological Diversity and Conservation 14: 385–389. https://doi.org/10.46309/biodicon.2021.952212

Özenirler Ç (2025) *Bombus* Latreille (Hymenoptera: Apidae) fauna of Beytepe Campus. In Proceedings of the 2nd International Paris Scientific Researches and Innovation Congress [Abstract/Oral Presentation], 505–506.

Pattrick JG, Symington HA, Federle W, Glover BJ (2020) The mechanics of nectar offloading in the bumble bee *Bombus terrestris* and implications for optimal concentrations during nectar foraging. Journal of the Royal Society Interface 17(162): 20190632. https://doi.org/10.1098/rsif.2019.0632

Percy DM, Cronk QC (2022) Psyllid honeydew as a *Bombus* food source in the boreal landscape. Ecological Entomology 47: 713–718. https://doi.org/10.1111/een.13147

Pfannenstiel RS (2015) Extended survival of spiders (Aranaeae) feeding on whitefly (Homoptera: Aleyrodidae) honeydew. Journal of Entomological Science 50: 110–118. https://doi.org/10.18474/JES14-08.1

Pringle EG, Novo A, Ableson I, Barbehenn RV, Vannette RL (2014) Plant-derived differences in the composition of aphid honeydew and their effects on colonies of aphid-tending ants. Ecology and Evolution 4: 4065–4079. https://doi.org/10.1002/ece3.1277

Rasmont P, Coppée A, Michez D, De Meulemeester T (2008) An overview of the *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae). In Annales de la Société entomologique de France. Vol. 44, No. 2. Taylor & Francis Group, 243–250. https://doi.org/10.1080/00379271.2008.10697559

Rasmont P, Ghisbain G, Terzo M (2021) Bumble bees of Europe and neighbouring regions. NAP Editions.

Rice KB, Eubanks MD (2013) No enemies needed: cotton aphids (Hemiptera: Aphididae) directly benefit from red imported fire ant (Hymenoptera: Formicidae) tending. Florida Entomologist 96: 929–932. https://doi.org/10.1653/024.096.0329

Sakagami K, Sugiura S (2018) A diverse assemblage of moths feeding on aphid honeydew. Journal of Asia-Pacific Entomology 21: 413–416. https://doi.org/10.1016/j.aspen.2018.01.019

Tena A, Pekas A, Wäckers FL, Urbaneja A (2013) Energy reserves of parasitoids depend on honeydew from non-hosts. Ecological Entomology 38: 278–289. https://doi.org/10.1111/een.12018

Ülgentürk S, Civelek H, Dostbil Ö (2021) Researches on bioecology of the giant pine scale, *Marchalina hellenica* Gennadius (Hemiptera: Marchalinidae) and relation with its predator *Neoleucopis kartliana* (Tanasijtshuk) (Diptera: Chamaemyiidae). Munis Entomology and Zoology 16: 1056–1069.

Wool D, Hendrix DL, Shukry O (2006) Seasonal variation in honeydew sugar content of galling aphids (Aphidoidea: Pemphigidae: Fordinae) feeding on Pistacia: host ecology and aphid physiology. Basic and Applied Ecology 7: 141–151. https://doi.org/10.1016/j.baae.2005.02.009